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Mating tactics of male feral goats (*Capra hircus*): risks and benefits.

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Fiona C. Saunders · Alan G. McElligott · Kamran Safi ·
Thomas J. Hayden

Mating tactics of male feral goats (*Capra hircus*): risks and benefits

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Abstract Intense competition between males for reproduction has led to the evolution of alternative mating tactics (AMTs). Feral goat males usually use a tactic called tending, in which they defend oestrous females from other males. Males may also use a second mating tactic called coursing, in which they gain access to oestrous females by disturbing a tending pair. Herein, we examine estimated mating success (EMS) and risks of using these tactics. Tending was only used by mature (≥ 4 years old), higher-ranking males and accounted for 75% of EMS. Coursing was used by males of all ages and dominance ranks, and accounted for 25% of EMS. Using coursing, male kids achieved 8% of EMS. Mature males achieved 92% of EMS. Both age and dominance rank were related to EMS, but age was not important after its relationship with dominance was controlled. Tending bouts were, on average, ca. 30 min long, while coursing bouts only averaged ca. 2 min. Males were more likely to suffer a butt while coursing than while tending, and formerly tending males were responsible for most butts. Kids that coursed had the highest risk of being butted. In most AMTs, there are reductions in the risks in relation to low fitness benefits. However, we found that the risks of butts during coursing were high, while our evidence suggests that the EMS was probably low. Nev-

ertheless, the existence of an effective AMT in male feral goats may have an important influence on the intensity of sexual selection and the effective population size.

Keywords Coursing · Dominance · Mating strategy · Mating success · Tending

Introduction

In polygynous mating systems, competition between males for access to females results in few males attaining most matings (Emlen and Oring 1977). When variance in male mating success is high, immature and/or subordinate males may be forced to defer reproduction or to adopt alternative mating tactics (AMTs). Game theory and the concept of evolutionary stable strategies (Maynard Smith 1982) have been used to explain both how AMTs evolve and persist. AMTs are governed by the characteristics of the males such as physiological condition, age and status. They are also flexible in that a male may be forced to use a low-payoff alternative tactic while immature but switch to the more common and usually more profitable tactic once mature.

Alternative mating tactics occur in a diverse array of species (Andersson 1994). AMTs have also been recorded in ungulates such as Soay sheep (*Ovis aries*, Preston et al. 2001), bighorn sheep (*Ovis canadensis*, Hogg 1984; Coltman et al. 2002) and topi (*Damaliscus lunatus*, Bro-Jørgensen and Durant 2003). In ungulates, competition from older dominant males means that immature and/or subordinate males usually do not mate, despite reaching full spermatogenic capacity while still immature, e.g. feral goats at 5 months (Ahmad and Noakes 1996). Most matings are therefore gained by large mature males, resulting in the deferral of reproduction for immature males unless they use AMTs (McElligott et al. 2001; Preston et al. 2003a).

Male goats may be under selective pressure to adopt AMTs. The main benefit is the realization of fitness at an early age, which is particularly important if the probability of survival to social maturity is low. The costs of such early

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F. C. Saunders · T. J. Hayden
Mammal Research Group, Department of Zoology,
National University of Ireland,
Dublin, Ireland

A. G. McElligott · K. Safi
Zoologisches Institut, Universität Zürich,
Zürich, Switzerland

A. G. McElligott (✉)
Verhaltensbiologie, Zoologisches Institut, Universität Zürich,
Winterthurerstrasse 190,
8057 Zürich, Switzerland
e-mail: amcellig@zool.unizh.ch
Tel.: +41-44-6355486
Fax: +41-44-6355490

involvement in breeding may be high, however, as competition with larger males may increase the risk of injury or death (Alvarez 1993; McElligott et al. 1998). Most AMTs have low associated costs or risks to balance the low fitness benefits expected relative to the primary mating tactic in use. AMTs that have high risks and high gains are rare (Austad and Howard 1984; Hogg 1984; Widemo 1998).

Feral goats are polygynous, and males use a non-territorial follower mating strategy. Dominance rank is considered the most important factor determining male mating success (Shackleton and Shank 1984; Dunbar et al. 1990). Two male mating tactics were identified in our study population: the formation of tending associations and coursing (Saunders 2000). Tending occurs when a dominant male remains close to an oestrous female and defends her from other males while allowing the female some freedom of movement (Hogg 1984). Coursing is a term first coined to describe an AMT of bighorn sheep, by which both immature and/or subordinate males try to obtain matings by separating oestrous females from the tending males (Hogg 1984).

In this study, we investigate the mating tactics of males in a feral goat population (1) to determine the relationship between mating tactics, age and dominance rank; (2) to estimate mating success achieved by each mating tactic; and (3) to measure the risks associated with each mating tactic.

Methods

Study area and population

We conducted the study on a population of feral goats in the Glendalough valley (ca. 220 ha) and surrounding reserve (2,200 ha) within the Wicklow Mountains National Park (53°0'N, 6°21'W), Wicklow, Ireland. The goats move down from the upland areas into the Glendalough valley for the breeding season and use two habitat types at this time: scree and cliff/heathland. The scree area is approximately 33 ha (15% of the valley), and the cliff/heathland area is approximately 58 ha (26% of the valley). A lake and a small road occupy the remainder of the valley (Saunders 2000).

There were 185 (123 females and 62 males) and 207 (128 females and 79 males) goats in the population during the breeding seasons in 1996 and 1997, respectively. The population structure of the males is given in Table 1. The median birth dates for kids were 19 February and 2 March

in 1996 and 1997, respectively (Saunders 2000). We considered three age classes of males in our study: kids, middle-aged males (1–3 years old) and mature males (≥ 4 years old). Ageing of goats was possible because they produce an annual ring on the horn sheath due to the slowing down or sometimes cessation of growth of the keratin during the winter months (Bullock and Pickering 1984).

All goats were individually recognizable using a combination of ear tags (50% of the population), coat colour and/or other natural markings. Goats were captured by herding into a corral on the valley floor. From there they were taken individually outside the corral and tagged with Allflex livestock tags (medium male size) using a standard tag applicator. Each goat was restrained for approximately 5–10 min without the use of tranquilizers by two to four people while tagging, and other checks were carried out. No goats were injured during capture and tagging, and all resumed their normal activities upon release.

Descriptions of the two mating tactics

Tending occurs when a male (the dominant male in the vicinity) maintains close proximity (approximately one body length) to an oestrous female and defends her from satellite males (subordinate males that are within approximately 10 m of the tending male), while allowing her relative freedom of movement (Hogg 1984). Tending males guard the female from the satellite males using horn threats and beard shakes, and if these fail, by rushing towards them.

Coursing occurs when one or more immature or subordinate males distract the tending male and/or harass the oestrous female, causing her to run and become separated from the tending male. Coursing males attempt to exploit the separation of the tending male from the oestrous female during this coursing chase to mate. This definition does not include the time when males accompany tending pairs and attempt to start a chase and, therefore, may underestimate the time that males spend coursing. If the tending male also chases the female, he then also becomes involved in a coursing bout. However, as he has been forced into chasing the female by the action of the other males, a formerly tending male (FTM) is not using the coursing tactic. The matings gained by these tending males that are forced to participate in coursing bouts are still considered to result from tending. The term “formerly tending male” is abbreviated as FTM in the remainder of the manuscript.

Table 1 Male population structure during the breeding season

	Kids	1	2	3	4	5	6	7	8	9	10	Total
1996	7	4	8	4	12	11	10	2	3	1	0	62
1997 ^a	23	7	3	7	6	9	10	10	1	2	1	79

Age is given in years. Kids refer to young of the year

^aIncludes three immigrants (one 1 year old, two 4 years old) from a neighbouring population that only remained in the area during the breeding season

Observations

The timing of the breeding season varied between years. We carried out searches of the study site for goat groups on most days during the pre-rut and rut. The pre-rut began approximately 3 weeks before the rut. The pre-rut was the period when males began to aggregate with the female groups and ended the day before the first mating was recorded in each year. The rut refers to the period when matings occurred. In 1996, the rut began on 18 September and ended on 7 October (duration, 20 days). In 1997, it began on 14 August and ended on 4 September (duration, 22 days). Our searches covered 70 and 55% of the days during the ruts in 1996 and 1997, respectively.

Once we located a group, we identified each goat. We always located as many females as possible on the search days (1996, females located on rut search days, mean=41.1, range=19–59, 33.4% of the total female population; 1997, females located on rut search days, mean=41.2, range=17–66, 32.2% of the total female population). If we found any female showing signs of oestrus, we then chose that female as a focal animal and carried out observations for at least 1 h on her and any other individuals that were nearby. However, most of our focal observations were far longer than 1 hour; on average, it was 4.4 and 3.0 h per focal female in 1996 and 1997, respectively. In 1996, we observed 25 oestrous females for 109 h, and 20 of those mated during our observations. In 1997, we observed 28 oestrous females for 85 h, and 18 of those mated during our observations. We observed an average of two oestrous females per day (mean=2.1, range=1–5). Oestrous females are obvious because they wag their tails frequently (Bullock 1991), and they are usually accompanied by at least one male (Dunbar et al. 1990).

We also recorded the use of male mating tactics and matings (ejaculations) within each observation period. Matings are obvious because a male mounts a female and jumps forward as it ejaculates. This is also the case when kids mate (see “Results”). In terms of mating tactics, we recorded 66 coursing bouts totalling 1.7 h in duration and 170 tending bouts totalling 86.5 h in duration. Our observations methods did not bias our results towards short tending bouts because our focal female observations (4.4 and 3.0 h average in 1996 and 1997, respectively) far exceeded the average length of tending bouts (see “Results”) and, indeed, were longer than the maximum length of any tending bout in either year (Saunders 2000). Females are usually not tended for the full duration of oestrus, and tending bouts are disrupted by, for example, other males or a tending male leaving a female to join another female. If a mating occurred, we continued observations for at least 30 min.

We recorded 28 and 27 matings during the 1996 and 1997 ruts, respectively. Overall, 38 females were observed mating during the 2 years: 18% (20/110) and 16% (18/115) of the females at least 1 year old. Most of these females (63.2%, 24/38) only mated once with one male, and some (23.7%, 9/38) mated more than once with the same male. Thus, 86.8% of females were monogamous. A small por-

portion (13.2%, 5/38) of females mated with two different males. We therefore use estimated mating success (EMS) in all the analyses and results. For example, if a male mated with one female either several times, or just once, and that female did not mate with any other males, the male was given an EMS of 1. If a female mated with two different males once each, those males were each given an EMS of 0.5.

We did not observe individual females for the full duration of oestrus, and therefore, it was possible that we underestimated the total number of males with which females mated. However, given the average length of focal observations (4.4 and 3.0 h for 1996 and 1997, respectively) it is likely that females do not mate as frequently as other ungulates with similar mating systems (Hogg and Forbes 1997; Coltman et al. 1999; Preston et al. 2003b). If they did, we would have expected to observe a far higher number of matings. In addition, our observations of mating are likely to give an accurate representation of the relative EMS of tending and coursing.

We recorded agonistic interactions (e.g. beard shakes, displacements, butts, horn threats, horn clashes and fights) between all individuals near the focal female and used the interactions between the focal female and males to determine the interaction rate between the oestrous female and males using each tactic. We calculated an index of dominance for all males using the results of the male–male agonistic interactions (Clutton-Brock et al. 1979). We assigned a rank of 1 to the male with the highest index value, and all other males were ranked accordingly. The dominance hierarchy was based on 779 and 1,176 agonistic interactions during the 1996 and 1997 ruts, respectively. Using this procedure, it was possible to calculate dominance ranks for 92 and 90% of males in 1996 and 1997, respectively. The remaining males in both years did not have enough interactions to allow a valid dominance rank to be calculated.

Our terminology regarding mating strategy and tactic follows Austad and Howard (1984). We used butts received from other goats as an indicator of the risks associated with using different mating tactics. Falls also occurred, but these were very rare (see “Results”).

Statistical analysis

We used SAS and SPSS for data analysis, with generalized linear models (GLMs) used for most of the analyses. We controlled for inflation in degrees of freedom in cases in which data were nested either within males that were present in both years or within observations by using repeated measures analysis in the “genmod” procedure of SAS. In so doing, we reduced the degrees of freedom of the models to the actual number of individual males in respect to the number of observations. This should be equivalent to taking males nested in years, e.g. as the error term in a classical multivariate statistical approach or in a mixed model. This approach allowed us (in cases in which we had correlated binary and/or count data) to select an appropriate link

function (link) for the GLMs and a response probability distribution (dist) to fit the models. We differentiated between the total number of butts received and the occurrence of butts to distinguish between factors determining the probability of observing butts during tending or coursing and factors determining the number of butts. Whereas the total number of butts gives the sum of all single butts observed during coursing or tending, the occurrence of butts represents a binary response variable (yes/no) describing the presence or absence of agonistic behaviour during an observation event. We used Spearman rank correlation for straightforward non-parametric correlations. Results were considered significant at the $p \leq 0.05$ level, and values are given as mean \pm standard deviation unless otherwise indicated.

Results

Mating tactics, age and dominance rank

Most males (65.2%, 92/141) participated in coursing and/or tending. Males of all ages participated in coursing: 63.3% (19/30) of kids, 57.6% (19/33) of middle-aged males (1–3 years old), and 60.3% (47/78) of mature males. Only males that were at least 4 years old tended, and 9.0% (7/78) mature males used this tactic only. We found that 29.5% (23/78) of mature males were involved in both coursing and tending, and 30.8% (24/78) were involved in coursing only.

Tending was only recorded for highly ranked males: those ranked 1 to 27 in 1996 and those ranked 1 to 30 in 1997. The number of tending bouts was negatively correlated with male dominance rank (Spearman rank correlation: $r_s = -0.58$, $n = 57$, $p < 0.001$, 1996; $r_s = -0.67$, $n = 71$, $p < 0.001$, 1997), indicating that higher-ranked males had higher numbers of tending bouts. By contrast, males of all ranks were involved in coursing bouts, and the number of coursing bouts was not related to dominance rank (Spearman rank correlation: $r_s = 0.09$, $n = 57$, NS, 1996; $r_s = -0.13$, $n = 71$, NS, 1997).

EMS, age and dominance rank

Overall, 25 mature males and 4 kids were observed to mate; the highest individual EMS for one male in 1 year was 5. No other immature males mated, although they were involved in coursing. Males aged between 5 and 7 years old had the highest EMS, with 6-year-olds being the most successful (total EMS for each cohort 3, 0, 0, 0, 4, 8, 10, 7, 4, 2 and 0 from kids to 10 years old, respectively; Fig. 1). Mature males achieved 92.1% (35/38) of EMS, and kids achieved 7.9% (3/38) of EMS. Dominance rank and age were highly related to one another (Spearman correlation coefficients: $r_s = 0.81$, $n = 128$, $p < 0.001$, Fig. 2), and both were also related to EMS when independently tested (type I sum of squares, data not shown). However, when the relationship between dominance rank and age was controlled in a repeated-measures GLM (with males as the

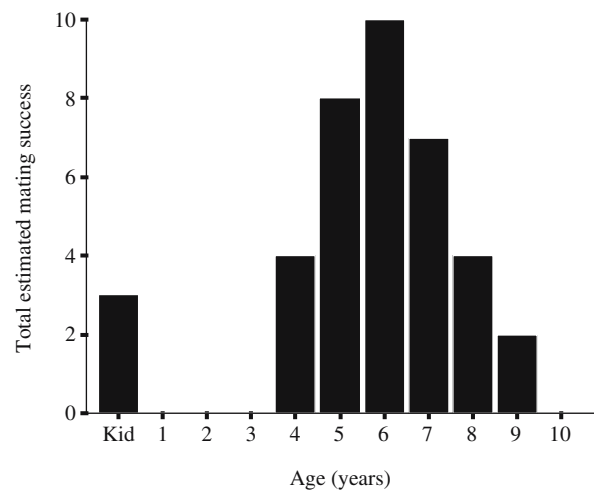


Fig. 1 The total estimated mating success for male feral goats of different ages

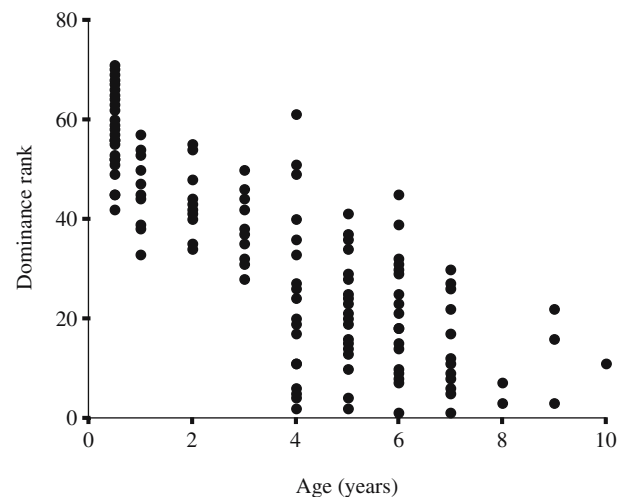


Fig. 2 The relationship between age and dominance rank

repeated subject) and using type III sum of squares, only dominance rank, and not age, was related to EMS (Table 2).

EMS, tending and coursing

Tending and coursing accounted for 75% (28.5/38) and 25% (9.5/38) of EMS, respectively. Independent of the

Table 2 Type 3 repeated-measures GLM of age, dominance rank and year, with estimated mating success as the dependent variable (dist=poisson, link=log, $N = 128$, $N_{\text{males}} = 84$, repeated subject, males)

	Mating success		
	<i>df</i>	χ^2	<i>p</i>
Age (years)	1	0.03	0.86
Dominance rank	1	5.79	0.02
Year	1	1.60	0.21

Dominance rank is the only predictor of estimated mating success after correcting for the effect of age and year

number of males using the tactic in a year, tending led to higher average EMS per male than coursing (GLM: dist=poisson, link=log, repeated subject=males; tending vs coursing: $df=1$, estimate=-0.64, $Z=-2.5$, $p=0.01$; covariate year: $df=1$, $\chi^2=0.4$, $p=0.54$). Males aged between 5 and 9 years had the highest estimated mating averages and the highest EMS as a result of tending (Fig. 3). However, the numbers of males participating at 8 and 9 years old were low at 2 and 3, respectively. The average EMS for kids as a result of coursing was similar to that for males aged between 4 and 7 years old (Fig. 3).

Duration and risks of tending and coursing

Tending bouts lasted, on average, $1,831 \pm 2,517$ s ($N=170$, min=7, max=14,295), whereas coursing bouts, with a mean duration of 94.4 ± 85.5 s ($N=66$, min=8, max=475), were far shorter (Kruskal-Wallis test: $\chi^2=100.7$, $df=1$, $p<0.0001$).

Butts occurred during only 5.9% (10/170) of tending bouts, and in each case, only one butt occurred during a bout (total butts=10). Butts occurred during 37.9% (25/66) of coursing bouts, and the total number of butts was 40. The probability of butts occurring was therefore significantly lower for tending than for coursing events (GLM: dist=binomial, link=logit; coursing vs tending: $df=1$, $\chi^2=24.7$, $p<0.0001$). The butts during tending were given by either the oestrous female or by other males (butts=5 in both cases), and the duration of a tending bout had no effect on the probability of a butt occurring (GLM: dist=binomial, link=logit, $N=170$; duration: $df=1$, $\chi^2=0.05$, $p=0.82$). Only two falls occurred (both during coursing), and these were not included in any of our detailed analyses.

The mean number of males involved in a coursing bout was $3.8 (\pm 1.8 \text{ SD}, n=66, \text{range } 1-10)$. Of the 66 coursing bouts, kids were involved 36 times, middle-aged males (1-3 years old) were involved 35 times, mature males (other than the FTM) were involved 53 times, and the FTMs were

involved 50 times. Within the 25 coursing bouts in which butts occurred, kids received 12 butts, middle-aged males received 1 butt, mature males received 9 butts and FTMs received 6 butts. The occurrence of a butt during a coursing bout was predicted by the coursing bout duration and not by the total number of males involved in a coursing bout (GLM: dist=binomial, link=logit; duration: $df=1$, $\chi^2=8.01$, $p=0.005$; number of males: $df=1$, $\chi^2=0.18$, $p=0.67$; Interaction not significant). However, neither duration nor the number of participating males influenced the total number of butts (for coursing bouts with total number of butts >0 ; GLM: dist=poisson, link=log; duration: $F_{1,22}=2.11$, $p=0.16$; number of males: $F_{1,22}=0.85$, $p=0.41$).

To test for age specific differences in the risk of receiving a butt during a coursing event, we applied a GLM in a repeated-measures design. In this model, we used for every age class a binary response variable indicating the occurrence of butt(s) to individuals of the respective age class, while using the coursing event as the repeated subject. The number of individuals belonging to the age classes (for $N>0$) and the duration of the coursing events were introduced as covariates to correct for their effect on the model. Age class, independent of the number of individuals belonging to that specific age class involved in the coursing event or the duration of the coursing event, had a significant influence on the model (GLM: dist=binomial, link=logit; age: $df=3$, $\chi^2=11.41$, $p=0.01$; number of individuals in an age class: $df=1$, $\chi^2=0.08$, $p=0.78$; and duration: $df=1$, $\chi^2=3.91$, $p=0.05$). This is due to the higher risk of receiving butts for kids relative to all other age classes (in 12 out of 36 times in which they participated; Table 3).

Most of the butts during coursing (48%, 19/40) were given by the FTMs to coursing males. Other butts were given by oestrous females to coursing males (20%, 8/40) and by coursing males to other coursing males (17.5%, 7/40). The remaining six butts (15%) were given to the FTMs either by the coursing males (4/40) or by the oestrous female (2/40). The FTMs gave significantly more butts to the coursing males than coursing males among each other (Table 4).

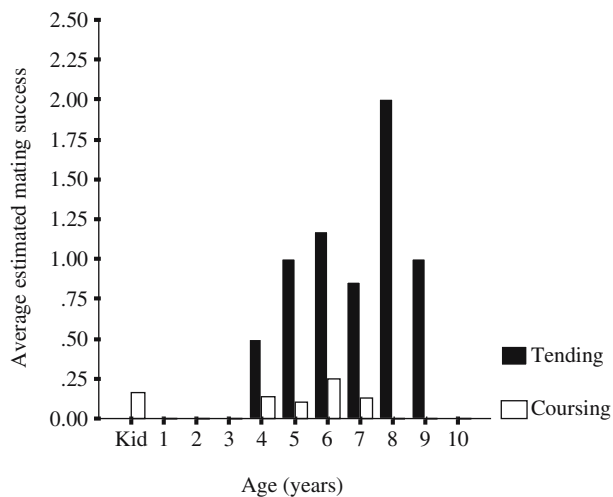


Fig. 3 Age-specific estimated mating success rates for tending and coursing; the total number of matings is divided by the number of males in each cohort that used the tactics

Table 3 Risks of receiving butts using post hoc parameter estimates (GLM: dist=binomial, link=logit, $N=25$ coursing bouts in which butts occurred)

	Occurrence of butts			
	Estimate	SE	Z	p
Kids	2.80	1.02	2.74	0.01
Middle-aged males	0	0		
Mature males	1.96	1.12	1.76	0.08
FTMs	1.60	1.10	1.45	0.15

Within age classes, comparisons are made with the middle-aged males as the least butted (one butt resulted from the 35 times in which they participated in a coursing event). The risk of receiving butts for kids is significantly higher compared to the risk of receiving butts for middle-aged males. The risk of FTMs and mature males receiving butts is not significantly increased in comparison to the middle-aged males
FTMs Formerly tending males

Table 4 Probability of giving butts using post hoc parameter estimates (GLM: dist=binomial, link=logit, $N=25$ coursing bouts in which butts occurred)

		Butts				
		<i>df</i>	Estimate	SE	<i>Z</i>	<i>p</i>
Classes of individuals giving butts	Coursing males	2	−1.42	0.72	−1.97	0.05
	Females	2	−1.26	0.70	−1.81	0.07
	FTMs		0	0		
Other effects in the model	Intercept	1	−0.29	0.46	−0.64	0.52
	Number of males	1	0.01	0.05	0.26	0.79
	Duration	1	<0.01	<0.01	0.54	0.60

Contrasts within the categories of males butting are calculated against the FTMs as the male category giving most of the butts. The probability of giving butts is significantly lower in coursing males compared to FTMs, which gave most of the butts observed. There is a tendency for females to give fewer butts than FTMs

FTMs Formerly tending males

Discussion

Tending was only used by mature (≥ 4 years old) and higher-ranking males and accounted for 75% of EMS. Coursing was used by males of all ages and dominance ranks and accounted for 25% of EMS. Male kids benefited from the use of coursing and were the only immature males that mated, achieving ca. 8% of EMS. Mature males achieved 92% of all EMS, but dominance rank was more important than age in determining this, presumably because only high-ranking males could tend females. The duration and risks of the two mating tactics also greatly differed. Tending bouts, which were far more successful in terms of matings, had an average duration of ca. 30 min, while coursing bouts were, on average, ca. 2 min long. However, males were far more likely to be butted while coursing than while tending. In addition, kids had the highest risk of being butted during coursing bouts, and FTMs gave most of these. In most AMTs, there are reductions in the risks of using these tactics, reflecting the low fitness benefits expected (Dominey 1984; Rubenstein 1984; Lucas and Howard 1995; Stockley et al. 1996). However, in our study population, the risks of butts associated with coursing were high, while our evidence suggests that the EMS of coursing males was probably low. This is in contrast to bighorn sheep, in which both risks and fitness benefits from using alternative tactics are considered to be high (Hogg 1984; Hogg and Forbes 1997; Pelletier 2005).

The mating system found in feral goats is an example of a conditional evolutionarily stable strategy (ESS). This consists of one mating strategy (non-territorial, follower), within which there are two tactics (coursing and tending) (Dunbar et al. 1990; Maynard Smith 1982; this study). Our study shows that these tactics potentially confer unequal average fitness, with EMS from tending far exceeding that from coursing. The adoption of a particular tactic is related to factors such as dominance rank, which is, in turn, related to age. Physical characteristics such as body size are also probably related to the adoption of particular tactics because these factors are all interrelated in males of polygynous ungulates (McElligott et al. 2001; Preston et al. 2003a).

Many AMTs are age-specific, and size dimorphism plays a key role in the evolution of AMTs. Males using alternatives are often smaller in size and more agile than those males using the primary mating tactic (Maynard Smith 1982; Gross 1996). On a few occasions in our study population, oestrous females that were being coursed ran into narrow channels between boulders in the scree, through which only kids could follow (F.C. Saunders, personal observation). They then became obscured from view. A similar occurrence has also been noted among feral goats on the island of Rum. There, oestrous females run into narrow cliff ledges, and large males (due to a combination of large body size and horn span) are unable to follow. Kids, however, can reach the females and may mate with them (D.J. Bullock, personal communication). Therefore, both small body size and agility are advantageous for coursing males, in a similar manner to immature bighorn sheep males (Hogg and Forbes 1997). Goat kids produce viable sperm (Ahmad and Noakes 1996), and therefore, it is likely that matings achieved by kids result in fertilizations. In Soay sheep (*O. aries*), lambs can also father a large proportion of offspring during some years (Stevenson and Bancroft 1995; Pemberton et al. 1999).

The risks and EMS resulting from coursing varied and depended on the ages of the males. A large number of males of all ages used coursing, but only some mated. Some kids gained a small proportion of EMS, but their risk of being butted was also highest. Other than kids, no other immature males mated, although a large number of them were involved in coursing. However, the risk of being butted was also low for these middle-aged males. Mature males achieved most EMS, and their risk of being butted was between that of kids and middle-aged males. In our study population, 77.8% (7/9) of all known causes of death are due to injury (44.4% broken legs, 33.3% due to falls; Saunders 2000), and being butted could increase the risks of falling from cliffs. The risk of injury while coursing has also been highlighted for bighorn sheep (Geist 1971; Festa-Bianchet 1987; Hogg and Forbes 1997), although sufficient quantitative data on butts and/or deaths to males using coursing and other tactics were not provided. However, in bighorn sheep, coursing rams fathered

44% of lambs, indicating that in this species, the potential benefits of coursing are far higher than in our study population (Hogg and Forbes 1997). By coursing, kids in our study achieved matings they might otherwise never attain because only 32% of males in our study population reach maturity (Saunders 2000).

In general, tending males received far less butts than coursing males, and also, tending males had lower rates of being butted even when they were forced to course. This was due mainly to two factors: FTMs were responsible for most butts, and oestrous females were more likely to direct aggressive actions towards other coursing males than towards FTMs. The mating behaviour of female feral goats therefore suggests an element of choice and is similar to the behaviour of bighorn sheep females (Hogg and Forbes 1997). It provides additional evidence for the role of female mate choice among ungulates that has, until recently, been considered of minor importance (Komers et al. 1999; Bro-Jørgensen 2002). Our observations also suggest a lower level of female promiscuity in our study population than in bighorn or Soay sheep (Hogg and Forbes 1997; Coltman et al. 1999; Preston et al. 2003b).

Our results, showing that tending males have the highest EMS and lower costs in terms of butts, are similar to recent evidence on the relationship between mating effort and mating success in other male mammals. Although males may incur substantial costs in terms of weight loss by engaging in reproductive activities (Yoccoz et al. 2002; Forsyth et al. 2005), this does not necessarily mean that successful males (in terms of matings) lose more weight than unsuccessful males. Male fallow deer (*Dama dama*) and brushtail possums (*Trichosurus vulpecula*) that mate do not incur greater energetic costs in terms of lost body weight than males that do not mate (McElligott et al. 2003; Isaac 2005). Similarly, in bighorn rams, the amount of time spent foraging during the rut was not constrained by the mating tactics (tending or coursing) adopted by males (Pelletier 2005). In this study, tending, which is the most successful tactic, was expected to result in higher costs in terms of reduced foraging time.

In conclusion, our results show that male feral goats use two distinct tactics (coursing and tending) to gain matings. Tending is by far the more successful strategy for achieving EMS. Coursing also results in EMS, but the risk of being butted associated with this mating tactic is higher than for tending. The existence of an effective AMT in male feral goats means that a few older dominant males do not monopolize mating success in a manner similar to other polygynous ungulates (McElligott and Hayden 2000). This is similar to findings for male bighorn and Soay sheep and has an important influence on the intensity of sexual selection and also the effective population size (Nunney 1993; Coltman et al. 1999, 2002). However, the level of promiscuous matings by females in our study was probably lower than in bighorn and Soay sheep, and therefore, the influence of sperm competition on male reproductive success is also likely to be lower (Hogg and Forbes 1997; Preston et al. 2003b).

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